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ORIGINAL ARTICLE

Male and female Blackbirds (*Turdus merula*) respond similarly to the risk of nest predation

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Abstract Several studies have found that adult birds of altricial species adjust their parental care behaviour (i.e. nest visits) in response to the current risk of predation for their offspring. However, no experimental study has so far investigated whether there are sex differences in these passive anti-predator responses during the nestling period. Differences between males and females could arise because of several factors, including (1) probability of detection, (2) confidence in parenthood, and (3) different parental care behaviour associated with each sex. To test whether these anti-predator passive responses involve sex differences, we experimentally manipulated the perceived risk of nest predation of adult Common Blackbirds (*Turdus merula*), a sexually dimorphic species with a relatively high extra-pair paternity level. Our results showed that nest predation significantly reduced adult visits to the nest, but not differentially between males and females, which does not support our predictions. Our findings suggest (1) that sex differences in predator-induced behaviour could depend on the type of response (active vs. passive anti-predator strategies); (2) the potential existence of a minimum threshold in detectability between males and females for these behavioural changes to occur; and (3) the contrasting and opposite effects of several factors that might impede the selection of sex differences in these types of parental care behaviour.

Keywords Nest predation · Parental care · Anti-predator strategies · Sex differences · *Turdus merula*

Zusammenfassung

Männliche und weibliche Amseln (*Turdus merula*) reagieren ähnlich auf das Nestprädationsrisiko

Mehrere Studien haben gefunden, dass Altvögel nesthockender Arten ihr Brutpflegeverhalten (d.h. Nestbesuche) an das momentan für ihre Nachkommen bestehende Prädationsrisiko anpassen. Bislang hat jedoch keine experimentelle Studie untersucht, ob es während der Nestlingsphase Geschlechtsunterschiede in dieser passiven Reaktion auf Nesträuber gibt. Unterschiede zwischen Männchen und Weibchen könnten aufgrund mehrerer Faktoren auftreten, einschließlich (1) der Wahrscheinlichkeit, entdeckt zu werden, (2) der Gewissheit der Elternschaft und (3) Unterschieden im Brutpflegeverhalten der Geschlechter. Um zu testen, ob sich die passive Reaktion auf Nesträuber zwischen den Geschlechtern unterscheidet, haben wir das von adulten Amseln (*Turdus merula*) wahrgenommene Nestprädationsrisiko experimentell manipuliert. Amseln weisen Sexualdimorphismus sowie relativ hohe Fremdvaterschaftsraten auf. Unsere Ergebnisse zeigten, dass Nestprädation die Nestbesuche der Altvögel signifikant reduzierte, jedoch nicht auf unterschiedliche Weise bei Männchen und Weibchen, was unseren

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Vorhersagen widerspricht. Unsere Befunde deuten darauf hin, dass (1) Geschlechtsunterschiede in durch Prädatoren hervorgerufenem Verhalten von der Art der Reaktion abhängen könnten (aktive im Gegensatz zu passiven Anti-Prädatorstrategien), (2) es möglicherweise eine Mindestschwelle gibt, jenseits derer sich Verhaltensunterschiede zwischen Männchen und Weibchen nachweisen lassen, und (3) widersprüchliche und entgegengesetzte Effekte mehrerer Faktoren die Selektion für Geschlechtsunterschiede in dieser Art des Brutpflegeverhaltens erschweren könnten.

Introduction

Nest predation represents an important source of natural selection across taxa (Ricklefs 1969; Martin 1995) and can influence variation in life-history strategies among birds in particular (reviews in Martin and Briskie 2009; Ibáñez-Álamo et al. 2015). Despite the increasing attention given by ornithologists in recent years, the effect of nest predation risk on birds' behaviour is not yet well understood (Ibáñez-Álamo et al. 2015). One of these major gaps in our knowledge is related to the role played by each sex and whether males and females are differentially affected by nest predation risk (Ghalambor and Martin 2002; Caro 2005). Sex differences in anti-predator responses have been more often studied in the context of adult predation risk and have been usually explained by sexual dimorphism or different activities delivered mainly by one of the sexes (i.e. singing behaviour by males) that usually increase the risk of predation (e.g. Caro 2005). Montgomerie and Weatherhead (1988) proposed several factors that could explain active anti-predator responses by adults against threats to their offspring (i.e. nest defence): (1) confidence of parenthood, (2) renesting potential, (3) perception of risk (i.e. sexual dichromatism or body dimorphism), (4) life-history characteristics (i.e. mortality rate) or (5) the ability to raise offspring unaided. Some of these factors may also be valid for passive anti-predator responses of adults in a context of nest predation risk (i.e. reduction of nest visits to avoid nest detection). For example, we could expect a lower anti-predator response in males than females because the confidence of parenthood is usually lower for males, and consequently the fitness costs associated with the loss of the clutch or brood are also reduced (Trivers 1972). Females are also more constrained in modifying their parental care behaviour in the presence of a nest predator than are males because nestling survival depends on certain tasks frequently attended only by females (e.g. brooding; Clutton-Brock 1991), and thus the trade-off between costs and benefits also changes according to the sex. Furthermore, under a high nest predation risk, passive parental anti-predator responses may differ for each sex due to different detectability probabilities for males and females. Evidence shows that conspicuous colours favour detectability (Cott 1940; Endler 1978; Cuthill et al. 2005; Ruiz-Rodríguez et al. 2013). In fact, males of many species have several adaptations to offset higher detectability by predators, such as singing from more concealed locations (e.g. Møller et al. 2008). This different detectability between sexes also affects parental provisioning in a context of adult-directed predation risk (Grunst et al. 2015), suggesting that it could also alter sex-specific parental care when the threat is directed at their offspring.

This sexual perspective has been partially investigated during incubation (Ghalambor and Martin 2000, 2002; Fontaine and Martin 2006; Massaro et al. 2008), but those studies have focused primarily on different approaches for each sex due to different sexual roles. For example, it is common to measure nest visit rate during incubation for males and the incubation bout length for females, since in many species, males feed the incubating female, which is the only sex that incubates (e.g. Ghalambor and Martin 2000; Fontaine and Martin 2006). This makes it difficult to compare the two sexes in order to identify differences in anti-predator behaviour. While several studies have demonstrated a reduction in offspring provisioning rates (e.g. Eggers et al. 2005, 2008; Massaro et al. 2008; Peluc et al. 2008; Zanette et al. 2011; Ghalambor et al. 2013; Hua et al. 2014; LaManna and Martin 2016), it remains unknown whether the reduction in nest visitation rates differs between sexes. Martin and Badyaev (1996) suggested that nest predation could place greater constraints on female than on male plumage brightness, implying that each sex responds differentially to nest predation risk. Another study on the sexually dimorphic Superb Fairy-wren (*Malurus cyaneus*) found that male, but not female, time at the nest predicted nest predation, this suggesting that the most conspicuous sex (usually the male) is selected to significantly reduce its parental care under the risk of nest predation to avoid revealing the location of the nest (Colombelli-Négrel and Kleindorfer 2010). Experimental studies in sexually dimorphic species during the nestling period would be most suitable to analyse these potential sexual differences, in particular in species where both the male and the female feed their chicks, since this allows comparisons of the same response in both sexes (i.e. change in nest visit rate). No previous experimental demonstration of this potential differential sexual behaviour in the context of nest predation is available, and this information is critical to understanding how each sex copes with the predation risk faced by their offspring.

Here, we manipulated the perceived predation risk of Common Blackbird (*Turdus merula*) nestlings in order to

test whether male and female anti-predator passive responses of adults differ under an scenario of threat directed to their offspring. Firstly, we predicted that the nest predation risk will reduce parental care at the nest to avoid revealing the location of the nest. Based on previous studies (see above), we expect a reduction in nest visit rate (prediction 1a), latency of the first visit (prediction 1b) and time feeding at the nest (prediction 1c). Secondly, we predicted that this reduction will be more extreme in males than in females because the former are the more conspicuous sex in this species and the latter is the only parent that broods the nestlings (predictions 2a–c). Alternatively, we could expect just the opposite pattern as the confidence of parenthood is lower for males than for females (predictions 3a–c).

Materials and methods

Species and area of study

The Common Blackbird is a medium-sized passerine widespread throughout Eurasia. It uses open cup nests, with both parents feeding their nestlings although only the female broods them (Cramp 1988). Each sex is easily distinguishable due to sexual dimorphism in colouration (Cramp 1988). Males are entirely black with yellow or orange-yellow bills and eyerings while females are brown, paler, and vaguely brown-mottled below, and with brown bills (Collar 2005). In fact, sexual dichromatism in this species has been suggested to be responsible for the higher predation suffered by Blackbird males (Christe et al. 2006). The Blackbird is a monogamous species but with a relatively high extra-pair paternity (29 % of broods; Creighton 2000). We made the study during the breeding seasons (May–July) of 2006 and 2007 in the Natural Park of Sierra Nevada, southern Spain (37°9′N, 3°24′W; 1050 m a.s.l.). The daily nest predation rate in this population is 0.08 (Ibáñez-Álamo and Soler 2010a).

Experimental design

We used a slight modification of the experimental procedure of Ibáñez-Álamo and Soler (2012). We actively looked for Blackbird nests in our study area. Once a nest was found, it was visited every 2 days to record the day of hatching. When chicks were 8 days old (±1 day), we manipulated the perceived risk of nest predation by simulating the presence of a Black-billed magpie (*Pica pica*) in the surroundings of the nest. Doing so, we controlled for nestling development and potential changes in anti-predator behaviour over the nestling period. At this age, chicks can partially thermoregulate (Rother 1987), which reduces the ethical problems of our experimental protocol that could keep parents away from the nest for some time. In addition, nestlings 8 days old are not fully developed to rely on their own anti-predator defences (e.g. leaving the nest) and still completely depend on their parents' protection against predators. We chose the magpie as the nest predator model because it is present in the study area (Ibáñez-Álamo and Soler 2010b), does not depredate adult Blackbirds, and is known to profoundly affect populations of this species by increasing nest predation (Groom 1993; Collar 2005). Nests were exposed for 3 h to a playback (one 15-s magpie call every 3 min) starting at daybreak. The recorder was placed 20 m from the nest and was changed every hour to simulate changes in the position of the predators. We used seven different magpie call recordings to prevent the Blackbirds from getting used to them and the potential problem of pseudoreplication. After the first hour of playback, when both adult Blackbirds were well aware of the increased nest predation risk, a video camera was placed near the nest (1.5–2.5 m) to film adult nest activity for the following 2 h. The control treatment consisted of the same manipulation protocol as for the experimental treatment but playing no sound. We did not use a manipulation control treatment, as no significant differences in anti-predator behaviour were observed for the same species between control (no sound) and the manipulation control (woodpigeon playbacks) treatments in a previous study (Ibáñez-Álamo and Soler 2012). Nests were exposed to each treatment on consecutive days, with half of the nests starting with the experimental treatment and the other half with the control treatment. From the video tapes, we noted the following variables for each sex: nest visit rate (number of parental visits per hour), time of latency (time since starting filming to the adult's first visit) and mean feeding duration (time from the start of feeding the first chick to the end of the last nestling fed during each visit). We also made a qualitative measure for the quantity of food delivered by Blackbirds by comparing the size of the food carried by adults with respect to their bill (range 1–5; 1 indicated smaller than half the bill size, 2 when the food was between half and the complete size of the bill, 3 represented the same size of the bill, 4 was assigned when food was between the size of the bill and double this size, and 5 when it was larger than double the size of the bill). The mean feeding duration was significantly correlated with the quantity of food delivered by the Blackbirds ($F_{1,44} = 5.62$, $r^2 = 0.35$, $P < 0.02$). Thus, we used this variable as a proxy for food provisioning.

Procedures used to explore the effect of predation risk usually involve taxidermic mounts of predators, but this can be problematic for several reasons (e.g. group mobbing effects) and the use of playbacks alone is recommended to solve such drawbacks (Ghalambor and Martin 2001). Indeed, birds can detect the presence of nest predators only by acoustic cues (reviewed in Lima 2009).

Statistical analysis

To determine the effect of nest predation risk on parental care behaviour, we used repeated-measure ANOVAs, since the same nest underwent different situations of nest predation risk on consecutive days. In all cases, treatment and sex were included as within-group factors. Year and treatment order were included in the model as between-group factors. The assumptions underlying the use of these analyses were systematically checked and the $\log_{10}$-transformation was applied when necessary. All statistical analyses were performed using STATISTICA ver. 8.0 software (StatSoft Inc. Tulsa, OK, USA). The values are reported as mean ± SE.

Results

We carried out the experiments in 26 different Blackbird nests. Overall, the parental nest visitation rate differed between treatments with a significant reduction in the high-risk situation ($F_{1,22} = 17.39$, $P = 0.0004$; Fig. 1), an effect consistent between years ($F_{1,22} = 0.01$, $P = 0.91$). However, when we tested this effect in relation to the sex (treatment × sex interaction), we found no significant effect ($F_{1,22} = 0.04$, $P = 0.84$), indicating that both males and females reduced their visits similarly.

In relation to time of latency, which would involve the willingness of parents to return to their nest after the placement of the video camera, we found no significant effect of treatment ($F_{1,11} = 2.95$, $P = 0.11$) or for the interaction between treatment and sex ($F_{1,11} = 0.72$, $P = 0.42$). No significant differences were found between years for this variable, either ($F_{1,11} = 0.01$, $P = 0.95$).

No significant effect of our treatment appeared for mean feeding time ($F_{1,11} = 0.33$, $P = 0.58$). However, we detected a marginal effect for the interaction between treatment and sex in this case ($F_{1,11} = 4.33$, $P = 0.06$), with females tending to reduce their time spent feeding under a high-risk situation but males increasing it (Fig. 2). As for the other variables analysed, this behaviour was not significantly different between years ($F_{1,11} = 0.50$, $P = 0.49$). Treatment order did not influence any of the variables analysed, as its effect was invariably nonsignificant (all $P > 0.05$).

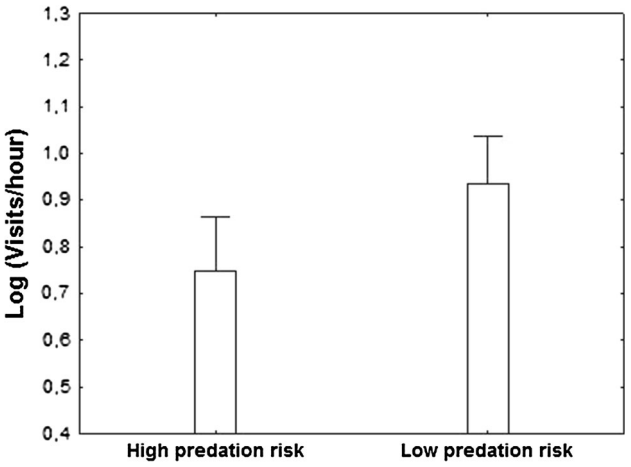

Fig. 1 Mean nest visit rate for each experimental treatment. *Bars* associated with each column denote the corresponding standard error

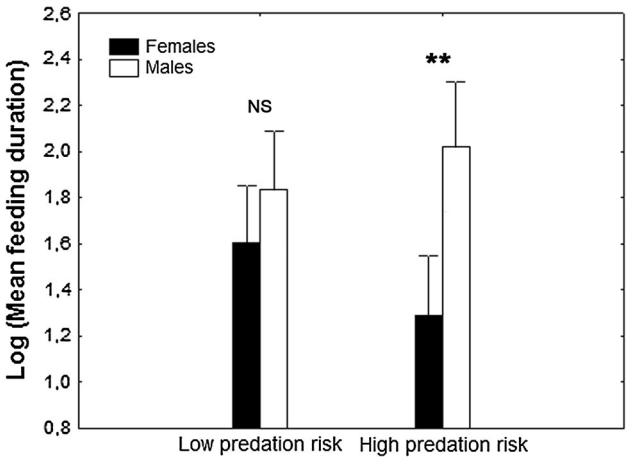

Fig. 2 Mean time spent by females and males feeding their nestlings per visit (time in seconds from the moment the adult inserted their beak into the mouth of the first chick fed until the adult finally removed it from the last nestling fed) in relation to the experimental treatments. *Bars* associated to each column denote the corresponding standard error. *NS* indicates non-significant differences between groups according to least significant difference (LSD) post hoc tests, while the *two asterisks* indicate significant differences with *P* values ≤0.005

Discussion

Our results showed a significant reduction in nest visits by adult Blackbirds under increased nest predation risk, fitting our prediction 1a. This agrees with previous studies on the topic (e.g. Eggers et al. 2005, 2008; Massaro et al. 2008; Peluc et al. 2008; Zanette et al. 2011; Ghalambor et al. 2013; Hua et al. 2014) and also with the reduction in nest visits observed for female Blackbirds during the incubation stage (Ibáñez-Álamo and Soler 2012). However, adult Blackbirds did not show an increase in latency time due to a high perceived predation risk (prediction 1b). This is surprising given that female Blackbirds in the same population significantly delayed their arrival to the nest while incubating (Ibáñez-Álamo and Soler 2012). Possibly, some anti-predator responses in adult Blackbirds are more relaxed by the end of the nesting period as the offspring start to develop other anti-predator defences by themselves (e.g. fleeing the nest under a predator attack). Alternatively,

this could be related to the fact that we quantified latency time from the placement of the camera rather than just after we started to manipulate the nest predation risk. It is possible that Blackbirds showed differences in latency time in this first non-filmed hour, although we think that it is unlikely given that in another study using the same experimental protocol we found that Blackbirds of the same population showed significant differences for this variable during the incubation stage (Ibáñez-Álamo and Soler 2012) which suggests that the effect of nest predation risk on latency time can be detected even without considering the first hour of manipulation. Contrary to our expectations (prediction 1c), we found no significant differences in mean feeding time between the situations of high and low nest predation risk. Nevertheless, these results support previous findings indicating that the key factor providing cues to potential predators are visits to the nest and not the activities within it (Montgomerie and Weatherhead 1988; Martin 1992). Alternatively, it has been proposed that not all traits have the same capacity to be plastic (e.g. Fontaine and Martin 2006; Kleindorfer 2007). Many variable factors modulate the visitation rate (e.g. food availability, predators, temperature) in comparison with feeding duration, and, thus, it could be adaptive to maintain a higher plasticity for the former than for the latter to adjust it depending on the situation.

Our results also showed that male and female Blackbirds respond similarly to the risk of nest predation, contradicting our predictions 2a–c and 3a–c, as we did not find significant sex differences for any of the variables considered. In a previous study, we found differences between sexes in nest visits during the incubation stage, but these could be explained by the fact that in this species, only females incubate and are not fed by males, so that the male seldom visits the nest during this stage (Ibáñez-Álamo and Soler 2012). For instance, another study also indicated that male and female Blackbirds responded similarly to the threat posed by a magpie in terms of the proportion of time spent hidden in the vegetation (Kryštofková et al. 2011). By contrast, these authors observed that males delivered the majority of active nest defence in comparison with females. All these pieces of evidence together indicate that both sexes respond similarly when using non-aggressive or passive anti-predator responses (i.e. by reducing their nest visits) but react differently when using aggressive or active anti-predator responses (i.e. attacks against predators).

Our findings, however, do not invalidate the hypothesis that the most conspicuous sex will respond less intensively to avoid revealing the location of the nest to nest predators. It is possible that there is a minimum threshold in colouration differences between sexes for this hypothesis to occur. Common Blackbirds are considered to have intermediate sexual dichromatism (Armenta et al. 2008). In contrast, the only evidence supporting this hypothesis came from an observational study with the Superb Fairy-wren (Colombelli-Négrel and Kleindorfer 2010), which is one of the most extreme dichromatic species analysed in a sample including over 900 species of birds (Armenta et al. 2008), thus implying the existence of such a threshold. Another potential explanation for the absence of sex differences in our study is the opposite selection played by the higher detectability of Blackbird males and their lower confidence of parenthood. These two factors acting simultaneously could cancel out each other. Additionally, we cannot rule out the possibility that other unconsidered factors (i.e. nest concealment) could have masked the effect of nest predation on parental care behaviour (e.g. Martin et al. 2000; Muchai and duPlessis 2005), thus preventing us from discerning significant differences between sexes even if they really existed.

The findings on feeding time are noteworthy but should be considered with caution given the marginally significant results. Males and females tended to invest the same amount of time to feed their nestlings in a situation of low nest predation risk (Fig. 2). However, males and females differed in their feeding time when there was an increased predation risk directed towards their offspring. This appears to be mainly a result of a reduction in female feeding time in a similar way as they reduce their on-bouts during incubation in such situations (Ibáñez-Álamo and Soler 2012).

In conclusion, our results indicate that the nest predation risk in Blackbirds significantly affect some aspects of parental care behaviour (i.e. nest visits), but not others (i.e. latency and feeding time). Moreover, male and female Blackbirds appeared to respond similarly in terms of their passive anti-predator responses when facing a high nest predation risk, in contrast to their differential sex role in active nest defence. Future studies on this topic should explore other species with larger differences in detectability (i.e. higher degree of sexual dichromatism) and confidence of parenthood between males and females in order to investigate the causes of sex-specific variation in anti-predator strategies in the context of nest predation.

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Compliance with ethical standards

Ethical standards The experiments on Common Blackbirds complied with the Spanish law on animal research and were approved by the regional government of Junta de Andalucía (RNM610). Ibáñez-Álamo et al. (2012) recommended that the effect of researcher disturbance on nest predation be studied for each model system, especially in those used to investigate avian nest predation per se. Following this recommendation, we tested the effect of our activity on Blackbird nests and found that we did not increase the nest predation rate in this species (Ibáñez-Álamo and Soler 2010a, b).

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